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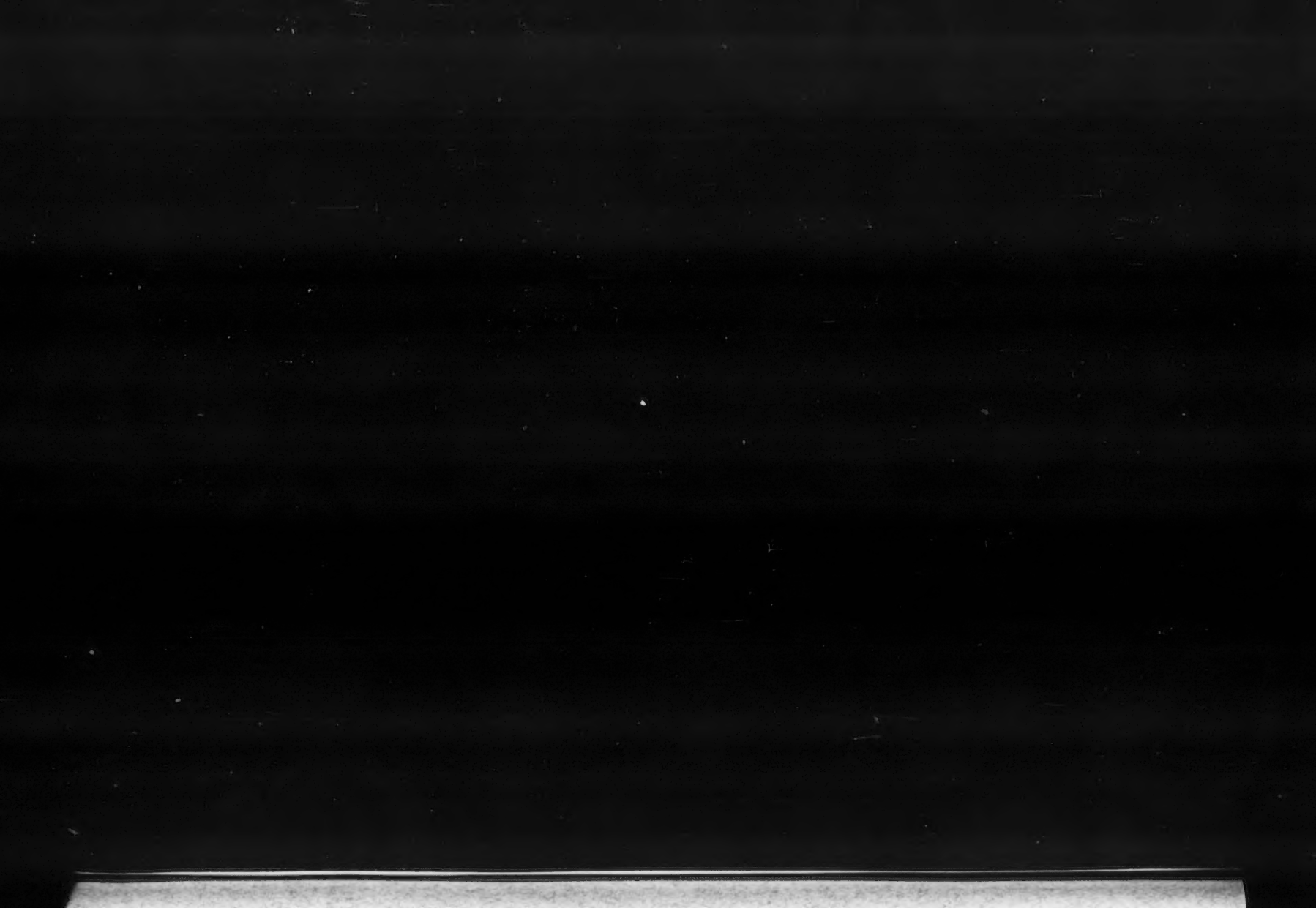

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BIOLOGICAL BULLETIN

INTER-PERIODIC CORRELATION IN THE ANALYSIS OF GROWTH.

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I. INTRODUCTORY.

In the literature of growth, mathematical equations to describe changes in the actual size of the organism, or changes in the growth rate, are finding continuously widening applications. One has merely to refer to the papers by Robertson, Miyake, Moeser, Ostwald, Reed and Holland (1919), and Reed (1920)[1] for illustrations.

The criticism usually directed against such work is that in the higher organism, growth is a highly complex process, and that in consequence it cannot be represented mathematically. It is because of the very fact that growth is a complex process that mathematical analysis of the experimental data is necessary. Corollary to this must be the recognition of the fact that since growth is not a simple process, no one mathematical formula will be adequate for full description[2] and no one method adequate for complete analysis.

Our purpose in the present note is to illustrate on a series of data collected by one of us (1919) the application of inter-periodic correlation coefficients to certain phases of the problem of growth.

Before passing to the analysis, which is the special purpose of this paper, definition of the terms which will be used and a note

[1] Citations of literature may be traced from Reed's paper.

[2] Those who consider the possible adequacy of a single equation take the ground that if it be possible to represent the growth of an organism by a simple equation, it may be by virtue of the fact that during growth the various (often conflicting external) factors which affect the living substance are integrated by the organism.

on the nature of the data on which the statistical methods are illustrated are in order.

By growth stage we mean any given moment of time at which a series of organisms are measured. It is, therefore, synonymous with age during the growth period. The absolute size of the organism or of one or more of its parts at a given growth stage is the only character of the organism available for consideration.

By growth period we understand the period of time elapsing between the sth and the $s+n$th growth stage.

The increase in size during any such period we shall designate as a growth increment.

By relative growth increment, i_{rs}, we understand the ratio of the growth increment, i, to the absolute size of the individual at stage, r, where r and s are any two successive stages.

Turning now to the question of the original data as given in Table I. of Reed's (1919) publication we note from a study of the physical constants for absolute size in Tables I. and II. that there is an increase in the mean height of the plants up to the 77th day.

TABLE I.

STATISTICAL CONSTANTS FOR SIZE AT VARIOUS GROWTH STAGES.

Growth Stage.	Mean.	Standard Deviation.	Coefficient of Variation.
7	17.931	1.617	9.0
14	36.328	4.786	13.2
21	67.845	8.932	13.2
28	97.672	14.673	15.0
35	130.724	19.174	14.7
42	168.707	24.801	14.7
49	205.397	32.760	16.0
56	229.672	37.842	16.5
63	247.345	42.574	17.2
70	251.776	43.433	17.3
77	253.810	43.767	17.2

The increase from the 63d to the 70th and from the 70th to the 77th day is relatively slight, being only 4.43 cm. or 1.79 per cent. of the height for the 63d day in the first case and only 2.03 cm. or 0.81 per cent. of the value for the 70th day in the second case. The difference between the 84th day and the 77th day is negligible. In view of the fact that there is no appreciable growth in

the sense in which the term is used here between the 77th and the 84th day, this period will be left entirely out of account in the calculation of the correlations for the following discussions.

Furthermore by considering the constants for growth increments as shown in Table II., we note that the coefficients of varia-

TABLE II.

STATISTICAL CONSTANTS FOR GROWTH INCREMENTS FOR VARIOUS GROWTH PERIODS.

Growth Period.	Mean Increment.	Standard Deviation.	Coefficient of Variation.
7 to 14.....	18.397	3.764	20.5
14 to 21.....	31.517	5.164	16.4
21 to 28.....	29.827	7.907	26.5
28 to 35.....	33.052	7.505	22.7
35 to 42.....	37.983	11.578	30.5
42 to 49.....	36.690	14.266	38.9
49 to 56.....	24.276	16.540	68.1
56 to 63.....	17.672	13.803	78.1
63 to 70.....	4.431	4.713	106.4
70 to 77.....	2.034	5.096	250.5

tion for growth increments from the 63d to the 77th day are abnormally great. This may be in part due to biological causes, but it is doubtless due to a considerable extent to the relatively large error of measurement when the increment is very small in comparison with the size of the organism. If this be true, we should expect the correlations for actual size for the 63d to the 84th day to be about the same as those for the immediately preceding growth stages, but the correlations for growth increments may be expected to be of little value.

The problems which may be considered will be presented and discussed seriatim.

II. ANALYSIS OF DATA.

PROBLEM I. *The correlation between the absolute size of the organisms at its several periods of development.*

When examined at an early stage of development, organisms are found to differ among themselves in size. The same is found to be the case when the same series is measured at a later growth stage or at maturity.

In the biological analysis of the phenomenon of growth a prob-

lem of great importance is that of the causes which bring about the differences in size observable at any stage of development, or after growth has entirely ceased. Are individuals which are found to be small at maturity those which were small initially and have remained so from the beginning, or may the growth rate of an individual change during the course of its development to such an extent that it may vary its position in the series under investigation from time to time? That the latter is to some extent the case we know from general observations on human children. The problem to be solved is that of the quantitative magnitude of the relationship between the size of the individual at different stages of development.

The nature of the biological problems to be investigated has been stated in earlier work, and an attempt has been made to solve them by grouping plants according to quintile (Pearl and Surface, 1915) or quartile (Reed, 1919) position in the culture to which they belong and ascertaining the quartile or quintile in which they fall at different stages of growth.

This method has the disadvantage that all the individuals, whatever their size, are lumped together in four or five groups. In this method of treatment, small differences between two individuals are, therefore, given as much significance as large ones, providing they are large enough to throw the two individuals into different quartiles or quintiles.

An alternative method, which will completely obviate this difficulty, is to determine the correlation between the sizes of the individual at different periods of growth. The possible correlations between the absolute size of the individuals in the 11 different stages of growth of the *Helianthus* plants are shown in Table III.

The coefficients in this table can be best understood by first examining those for the relationships between the sizes of the plants near the period of maturity, and then passing to the relationships between the sizes of the plants at earlier stages.

Considering first of all the coefficients in the lower right-hand corner of the table, we note that all the coefficients are very high, denoting practically perfect correlation. This is the relationship which would be expected for a period when the organism has

TABLE III.

CORRELATION BETWEEN THE ACTUAL HEIGHT OF THE PLANTS AT THE VARIOUS GROWTH STAGES.

Stage.	Stage.										
	7	14	21	28	35	42	49	56	63	70	77
7		+.733 ±.041 17.9	+.558 ±.061 9.14	+.468 ±.069 6.78	+.347 ±.078 4.46	+.193 ±.085 2.26	+.130 ±.087 1.50	+.093 ±.088 1.05	+.069 ±.088 0.78	+.065 ±.088 0.74	+.053 ±.088 0.60
14	+.733 ±.041 17.9		+.889 ±.019 48.0	+.695 ±.046 15.2	+.532 ±.064 8.38	+.343 ±.078 4.39	+.220 ±.084 2.60	+.151 ±.087 1.74	+.150 ±.087 1.73	+.140 ±.087 1.62	+.123 ±.087 1.41
21	+.558 ±.061 9.14	+.889 ±.019 48.0		+.887 ±.019 47.1	+.739 ±.040 18.4	+.552 ±.062 8.97	+.390 ±.075 5.20	+.320 ±.080 4.02	+.311 ±.080 3.90	+.297 ±.081 3.67	+.282 ±.082 3.46
28	+.468 ±.069 6.78	+.695 ±.046 15.2	+.887 ±.019 47.1		+.936 ±.011 85.2	+.752 ±.038 19.6	+.534 ±.063 8.44	+.409 ±.074 5.55	+.356 ±.077 4.61	+.329 ±.079 4.17	+.318 ±.080 3.99
35	+.347 ±.078 4.46	+.532 ±.064 8.38	+.739 ±.040 18.4	+.936 ±.011 85.2		+.892 ±.018 49.5	+.674 ±.048 13.9	+.488 ±.067 7.24	+.394 ±.075 5.26	+.350 ±.078 4.50	+.333 ±.079 4.23
42	+.193 ±.085 2.26	+.343 ±.078 4.39	+.552 ±.062 8.97	+.752 ±.038 19.6	+.892 ±.018 49.5		+.914 ±.015 62.5	+.732 ±.041 17.8	+.629 ±.053 11.8	+.580 ±.059 9.86	+.558 ±.061 9.16
49	+.130 ±.087 1.50	+.220 ±.084 2.60	+.390 ±.075 5.20	+.534 ±.063 8.44	+.674 ±.048 13.9	+.914 ±.015 62.5		+.900 ±.017 53.5	+.819 ±.029 28.1	+.775 ±.035 21.9	+.758 ±.038 20.1
56	+.093 ±.088 1.05	+.151 ±.087 1.74	+.320 ±.080 4.02	+.409 ±.074 5.55	+.488 ±.067 7.24	+.732 ±.041 17.8	+.900 ±.017 53.5		+.948 ±.009 105	+.926 ±.013 73.3	+.911 ±.015 60.2
63	+.069 ±.088 0.78	+.150 ±.087 1.73	+.311 ±.080 3.90	+.356 ±.077 4.61	+.394 ±.075 5.26	+.629 ±.053 11.8	+.819 ±.029 28.1	+.948 ±.009 105		+.994 ±.001 970	+.986 ±.002 411
70	+.065 ±.088 0.74	+.140 ±.087 1.62	+.297 ±.081 3.67	+.329 ±.079 4.17	+.350 ±.078 4.50	+.580 ±.059 9.86	+.775 ±.035 21.9	+.926 ±.013 73.3	+.994 ±.001 970		+.993 ±.001 828
77	+.053 ±.088 0.60	+.123 ±.087 1.41	+.282 ±.082 3.46	+.318 ±.080 3.99	+.333 ±.079 4.23	+.558 ±.061 9.16	+.758 ±.038 20.1	+.911 ±.015 60.2	+.986 ±.002 411	+.993 ±.001 828	

practically attained its adult size and in which there is relatively little change from one week to another.

As we follow the correlations between the later periods and preceding periods back, we note that there is a regular decrease in the values of the correlation coefficients. This may be best shown by summarizing the results graphically in diagram 1.

In the graph the correlation of the size of the organism at each

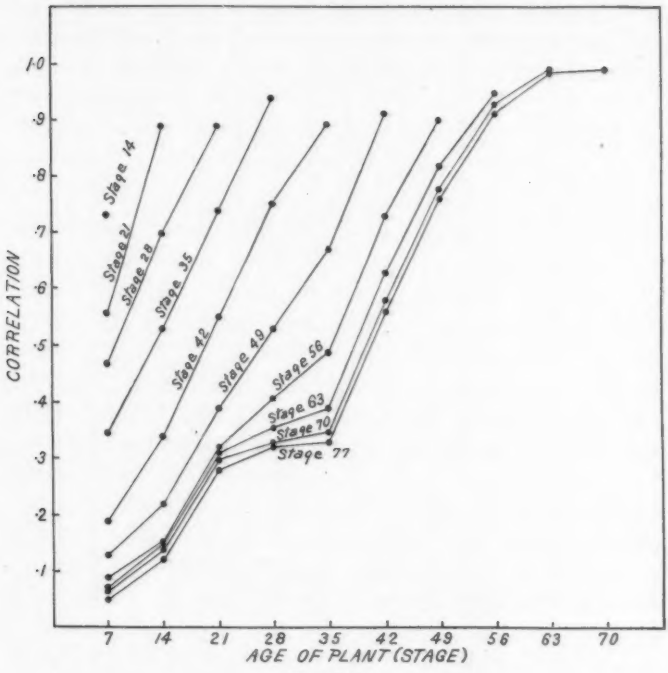

DIAGRAM 1.

growth stage with its size at every antecedent growth stage (shown at the bottom of the diagram) is shown on the scale of correlation at the left by points marking the magnitude of the correlations for each of the growth stages. The pitch of the lines connecting the points for the 14th to the 77th growth stage shows the rapid decrease in the magnitude of the correlations as the stages become more widely separated in time.

The same type of diagram may be used to show the relationship between the size at early and at later growth stages. Diagram 2 shows the distribution of the magnitudes of the correlations for sizes of the individuals at the 7th to the 70th day (stage) and the size at subsequent growth stages.

From these lines it is clear that the correlations between size

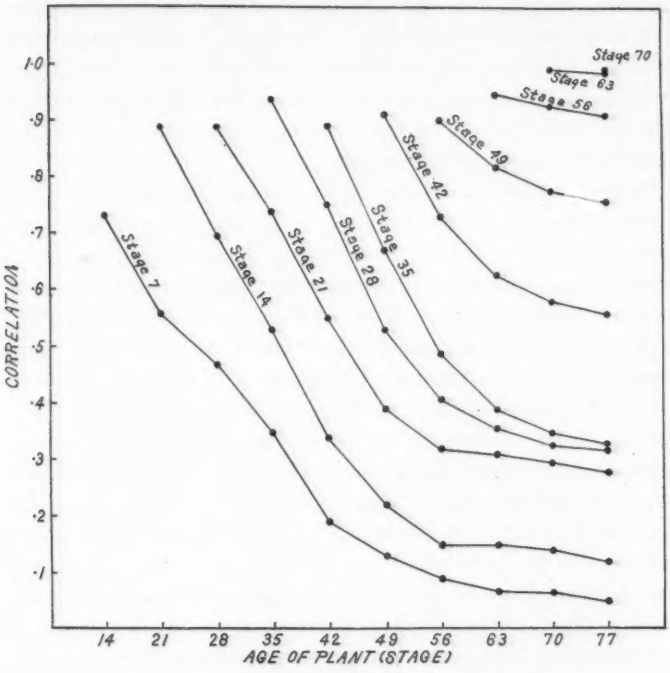

DIAGRAM 2.

at antecedent and subsequent periods decrease as the periods become more widely separated in time. This is true without exception for every period which furnishes evidence upon the question.

The coefficients are, however, positive in sign throughout, thus suggesting (though in some cases not proving) that throughout its growth period the size of the plant bears some relation to its size when first measured. This result is in agreement with the

findings of Webber (1920) in regard to the growth of *Citrus* stock.

PROBLEM 2. *The correlation between the growth increments of the organism during the several growth periods.*

Our second problem is to determine whether there is a correlation in growth increments as well as in actual size of the organism. We shall thus answer the question whether the organism which grows more rapidly than the average during one growth period will grow more rapidly than the average in other growth periods and whether the organism which lags behind the average in its rate of growth during one growth period will also lag behind during other growth periods.

Little has heretofore been done towards the statistical treatment of growth increments. This is probably in part due to the arithmetical difficulties of computing the constants for increments, but if the moments and product moments be taken about zero as origin in computing the coefficients required under Problem 1 above, the calculations for growth increments are easily made by the use of formulæ given elsewhere (Harris, 1920).

The symmetrical table showing the relationship between the actual growth increments for all of the combinations of growth periods appears as Table IV. This table shows positive and statistically significant correlation coefficients for closely associated periods throughout the season up to and including the period for the 63d to the 70th day. The coefficients for the period from the 70th to the 77th day cannot in general be considered statistically significant in comparison with their probable errors.

Examining these results in a little greater detail, we note that the nine coefficients showing the relationship between the growth increments of successive weeks (the constants bordering the diagonal cell of the symmetrical table of constants) are all positive in sign and with the exception of the last (showing the relationship between the growth of the period from the 63d to 70th and that between the 70th to 77th day) all are statistically significant. The eight coefficients measuring the correlations between the growth increments of weekly periods which are separated by one week are also without exception positive, but are lower in magnitude and less certainly statistically significant. For periods more

TABLE IV.

CORRELATIONS BETWEEN THE GROWTH INCREMENTS DURING THE SEVERAL GROWTH PERIODS.

Growth Period.	Growth Period.									
	7 to 14.	14 to 21.	21 to 28.	28 to 35.	35 to 42.	42 to 49.	49 to 56.	56 to 63.	63 to 70.	70 to 77.
7 to 14...		+.655±.051 12.9	+.259±.083 3.14	+.013±.089 0.14	−.115±.087 1.32	−.102±.088 1.17	−.095±.088 1.08	+.082±.088 0.93	−.070±.088 0.79	−.136±.087 1.57
14 to 21...	+.655±.051 12.9		+.630±.053 11.8	+.264±.082 3.21	+.064±.088 0.73	−.024±.089 0.27	+.011±.089 0.13	+.100±.088 1.14	−.082±.088 0.93	−.047±.088 0.53
21 to 28...	+.259±.083 3.14	+.630±.053 11.8		+.636±.053 12.1	+.161±.086 1.86	−.079±.088 0.90	−.179±.086 2.08	−.140±.087 1.61	−.249±.083 2.99	−.023±.089 0.26
28 to 35...	+.013±.089 0.14	+.264±.082 3.21	+.636±.053 12.1		+.532±.064 8.37	+.147±.087 1.70	−.316±.080 3.96	−.273±.082 3.33	−.483±.068 7.12	−.169±.086 1.97
35 to 42...	−.115±.087 1.32	+.064±.088 0.73	+.161±.086 1.86	+.532±.064 8.37		+.778±.035 22.3	+.070±.088 0.79	+.067±.088 0.76	−.189±.085 2.21	−.106±.088 1.21
42 to 49...	−.102±.088 1.17	−.024±.089 0.27	−.079±.088 0.90	+.147±.087 1.70	+.778±.035 22.3		+.416±.073 5.67	+.250±.083 3.01	−.005±.089 0.06	+.038±.088 0.43
49 to 56...	−.095±.088 1.08	+.011±.089 0.13	−.179±.086 2.08	−.316±.080 3.96	+.070±.088 0.79	+.416±.073 5.67		+.299±.081 3.70	+.453±.070 6.44	+.022±.089 0.25
56 to 63...	+.082±.088 0.93	+.100±.088 1.14	−.140±.087 1.61	−.273±.082 3.33	+.067±.088 0.76	+.250±.083 3.01	+.299±.081 3.70		+.476±.069 6.91	+.188±.085 2.20
63 to 70...	−.070±.088 0.79	−.082±.088 0.93	−.249±.083 2.99	−.483±.068 7.12	−.189±.085 2.21	−.005±.089 0.06	+.453±.070 6.44	+.476±.069 6.91		+.086±.088 0.97
70 to 77...	−.136±.087 1.57	−.047±.088 0.53	−.023±.089 0.26	−.169±.086 1.97	−.106±.088 1.21	+.038±.088 0.43	+.022±.089 0.25	+.188±.085 2.20	+.086±.088 0.97	

widely separated in time the correlations are in part positive and in part negative in sign.

Thus from the results as a whole it appears that the increments of successive periods are generally positive and fairly highly correlated when the periods show actual growth increments. Thus the zone of coefficients lying along the diagonal cell are positive and generally fairly high. When the periods are separated by any considerable length of time the coefficients are generally insignificant in magnitude and may, as a matter of fact, be either positive or negative in sign.

The relationship may be brought out by determining the averages of the correlation coefficients, with regard to sign, for the increments of periods separated by various lengths of time. The results are as follows.

Period of Separation (Weeks).	Number of Correlations Averaged.	Average Correlation.
0	9	+.5009
1	8	+.2240
2	7	—.0334
3	6	—.1236
4	5	—.1640
5	4	—.1033
6	3	—.0077
7	2	—.0585
8	1	—.1360

If we disregard the cases in which there are less than five coefficients to be averaged, we note a steady decrease in the magnitude of the correlation coefficient. Periods of growth which are successive or separated by only one week have positively correlated growth increments. Periods which are more widely separated show negative correlations of the increments.

The relationship between the coefficients in Table IV. may be clarified by diagram 3 which shows the relationship between four of the ten growth increments and each of the other ten increments. The increments selected as a "first variable" in the correlation are the first, fourth, seventh, and tenth. This has the advantage of representing the first and the last growth increment, and of leaving undrawn no more than two successive increments. The figures are aligned according to the ten increments representing the "second variable" of the correlation.

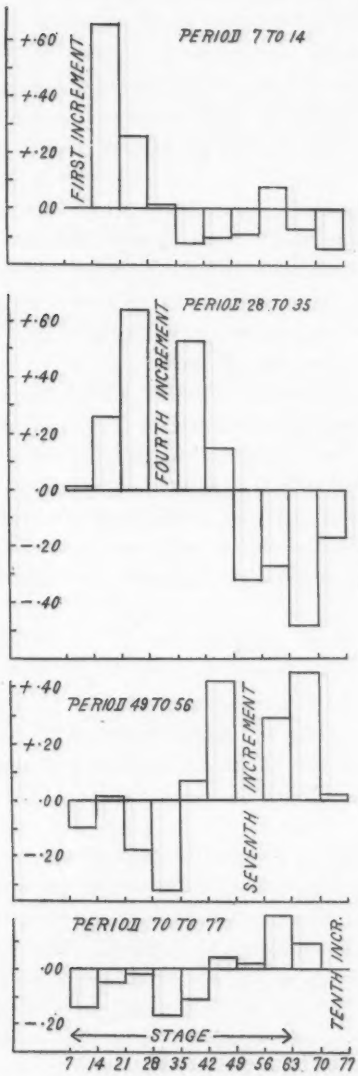
PERIOD 7 TO 14
FIRST INCREMENT
+·60
+·40
+·20
00
PERIOD 28 TO 35
FOURTH INCREMENT
+·60
+·40
+·20
·00
−·20
−·40
PERIOD 49 TO 56
SEVENTH INCREMENT
+·40
+·20
·00
−·20
PERIOD 70 TO 77
TENTH INCR.
·00
−·20
STAGE
7 14 21 28 35 42 49 56 63 70 77

DIAGRAM 3.

The graphs for the first, fourth and seventh increment show clearly the shift in the position of the maximum positive correlation from the earlier to the later periods as the "first variable" is chosen from the later periods. The same is shown less clearly by the correlations for the tenth increment, but there the coefficients are very small, presumably because growth has practically ceased.

It is clear, therefore, that plants which are growing more rapidly during any period of development will grow more rapidly during a closely associated subsequent period of development but that there is little or no relationship, or even a negative relationship, between the rate of growth of the organisms studied at considerably separated periods of time.

Since the correlations for absolute growth increments are so small for all except successive periods of time, it seems unnecessary to deal at present with the relative growth increments, *i.e.*, with the growth increments expressed as a fraction of the size of the organisms at the beginning of the growth period.

PROBLEM 3. *The correlation between the absolute size of the organism at given stages of development and subsequent growth increments.*

In the higher plant organism rate of growth at any period must be supposed to depend to some extent upon plastic materials synthesized by the more nearly mature portions of the same individual. Thus one might expect to find a relationship between the actual size of the organism at any stage of growth and the rate at which the organism increases in size during a subsequent period.

We have determined the possible correlations between the absolute size of the organism at different periods and the growth increment of the organism during subsequent growth periods. The coefficients are presented in Table V. This shows positive correlation between the actual size of the organism at every stage of development from the 7th to the 70th day and the increase in the size of the organism during the following week. The magnitude of the correlation is of the order $r = 0.45$ to $r = 0.60$ for the 7th, 14th, 21st, and 28th day. For these growth stages the correlation between actual size and the subsequent growth incre-

TABLE V.

CORRELATIONS BETWEEN HEIGHT AT EACH GROWTH STAGE AND THE INCREMENTS AT SUBSEQUENT GROWTH PERIODS.

Stage.	Growth Period.									
	7 to 14.	14 to 21.	21 to 28.	28 to 35.	35 to 42.	42 to 49.	49 to 56.	56 to 63.	63 to 70.	70 to 77.
7	+.503 ±.066 7.60	+.285 ±.081 3.50	+.239 ±.084 2.86	−.028 ±.089 0.32	−.162 ±.086 1.88	−.036 ±.088 0.41	−.046 ±.088 0.52	−.042 ±.088 0.47	−.021 ±.088 0.24	−.100 ±.088 1.14
14		+.611 ±.056 11.0	+.285 ±.081 3.50	+.000 ±.089 0.01	−.146 ±.087 1.68	−.093 ±.088 1.06	−.090 ±.088 1.03	+.050 ±.088 0.57	−.062 ±.088 0.70	−.141 ±.087 1.63
21			+.517 ±.065 7.96	+.153 ±.087 1.77	−.041 ±.088 0.46	−.063 ±.088 0.72	−.042 ±.088 0.48	+.084 ±.088 0.96	−.081 ±.088 0.92	−.103 ±.088 1.18
28				+.436 ±.072 6.08	+.062 ±.088 0.70	−.081 ±.088 0.92	−.122 ±.087 1.40	−.024 ±.089 0.27	−.183 ±.086 2.14	−.075 ±.088 0.85
35					+.255 ±.083 3.09	−.004 ±.089 0.05	−.217 ±.084 2.57	−.125 ±.087 1.43	−.329 ±.079 4.17	−.124 ±.087 1.42
42						+.360 ±.077 4.67	−.135 ±.087 1.56	−.065 ±.088 0.74	−.343 ±.078 4.39	−.145 ±.087 1.67
49							+.079 ±.088 0.89	+.059 ±.088 0.67	−.262 ±.083 3.17	−.093 ±.088 1.06
56								+.182 ±.086 2.12	−.029 ±.089 0.32	−.071 ±.088 0.81
63									+.129 ±.087 1.48	−.002 ±.089 0.03
70										+.007 ±.089 0.08

ment is clearly significant in comparison with its probable error. The coefficients are lower for the 35th and the 42d day, but are probably statistically trustworthy. Beyond this period there seems to be no relationship between the size of the organism and its growth rate in an immediately following period.

For the first two stages of growth measured, the 7th and the 14th day, there may be a significant correlation of the order $r = +.285$ between size and growth increments during the second following week.

The coefficient of correlation between size and the increment in the second week following is also positive for the 21st and 28th day, but neither of these values may be considered statistically significant in comparison with its probable error. Finally for the first stage (seventh day) there may be a significant correlation between absolute size and growth increments during the third week following ($r = +.239$ for increment for 21st to 28th day). Other than this the coefficients are for the most part statistically insignificant in comparison with their probable error.

Summarizing the preceding statements as a basis for further analysis, we note that for the first six growth stages (7th to 42d day) there is a significant positive correlation between the size of the organism at the given stage and the growth increment of the following week. For the first two growth stages (and possibly in the third where $r/E_r = 1.77$) there is a significant correlation between the size of the organism and the growth increment in the second subsequent week. Finally, for the first stage only, there is a significant positive correlation between size and growth increment in the third subsequent week.

Disregarding these 9 coefficients and the 4 positive but not significant correlations between the sizes at the several growth stages and the growth increments of the following week, we may note the following facts concerning the remaining 42 coefficients.

Of these 42 coefficients 36 are negative while only 6 are positive in sign. Of the 6 positive coefficients only that between actual size on the 21st day and growth increment between the 28th and 35th day (already considered above) is as large as its probable error. Of the 36 negative coefficients 18 are larger than

their probable error, and 5 of these are over twice as large as their probable error.

There is, therefore, clear evidence that the subsequent growth of the higher plant organism is measurably conditioned by its size. In general the larger individuals grow more rapidly in immediately subsequent periods, but somewhat more slowly than the average in more distant subsequent periods.

While a detailed discussion of the relation of these results to the theory that growth may be satisfactorily described by the curve of an autocatylic reaction falls quite outside the scope of this paper, it must be noted that negative correlations between actual size at a given stage and the growth increments of certain subsequent growth periods might be expected. As Reed and Holland (1919) have pointed out the plants attained about half their final height at about the thirty-fourth day. From this time on the increments were decreasing. Plants which had attained more than the average size at this period would, therefore, of necessity, make smaller average increase in size in later periods.

The number of individuals measured is not sufficiently large to carry the analysis farther.

III. Recapitulation.

The purpose of this paper has been to illustrate on the basis of a specific series of data the value of the inter-periodic correlation coefficient in the analysis of the phenomena of growth.

The analysis shows that in the case of a series of *Helianthus* plants the actual size of the individual at any stage of development is closely correlated with its size at other closely associated stages of development. The magnitude of the correlation rapidly diminishes as the growth stages become more widely separated in time. Thus the final size of the organism is but to a slight extent determined by its initial size.

The correlation between successive growth increments is positive in sign and statistically significant, with the general average of $\bar{r}=.501$. The correlation for increments of weekly periods separated by one week is on the average only about $\bar{r}=.225$. For periods more widely separated than this the correlation between growth increments is on the average negative in sign.

Thus plants which are growing more rapidly during one period of development will grow more rapidly during a closely associated period, but there is little or no relationship between the growth increments of more widely separated periods.

The growth increment of the organism is positively correlated with its size at an immediately preceding stage. In the early stages of growth, the growth increments of two or even three subsequent periods are positively correlated with the initial size of the organism.

LITERATURE CITED.

Harris, J. Arthur.

'20 Formulæ for the Calculation of the Correlations of Size and of Growth Increments in the Developing Organism. Proc. Soc. Exp. Biol. and Med. *In press.*

Pearl, R., and Surface, F. M.

'15 Growth and Variation in Maize. Zeitschr. Indukt. Abst. u. Vererbungslehre, 14: 97–203.

Reed, H. S.

'19 Growth and variability in *Helianthus.* Amer. Jour. Bot., 252–271.

'19 The Growth Rate of an Annual Plant, *Helianthus.* Proc. Nat. Acid. Sci., 5: 135–144.

Reed, H. S.

'20 The Nature of the Growth Rate. Jour. Gen. Physiol., 2: 545–561.

Webber, H. J.

'20 Selection of Stocks in *Citrus* propagation. Bull. Univ. Calif. Coll. Agr., 317

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THE CHROMOSOMES OF PSEUDOCOCCUS NIPÆ.

FRANZ SCHRADER,

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INTRODUCTION.

In the course of some work on sex determination in the different species of *Pseudococcus*—a genus of the Homoptera—very peculiar conditions were met with in the chromosome behavior. These peculiarities were observed especially in *Pseudococcus nipæ* (identified by H. Morrison, Bureau of Entomology), and it is of this species that the present account is given. A more detailed report, covering other species of *Pseudococcus* as well, is reserved for a later paper.

Most of the material was fixed in Allen's modification of Bouin's fluid. On the whole, fixation is more or less difficult; and at best the cells are somewhat small. The main features are clear cut, however, and hardly to be mistaken. I am indebted to Professor E. B. Wilson and to Professor C. E. McClung who examined some of my slides and offered helpful criticism.

THE CHROMOSOMES IN THE FEMALE.

The number of somatic chromosomes in the female is ten, with little or no size and form differentiation. Counts are made with little difficulty in various cells, but oögonial cells furnish of course the best criterion. Generally the chromosomes are counted most easily just before they have become arranged in a metaphase plate. There can be no doubt as to their number (Fig. 6). A detailed study of the maturation phenomena in the female was not made. Suffice it to say that five tetrads are formed and that these are normal in appearance; they are very much like those formed in the oögenesis of many other Homoptera (Fig. 7). The reduction process is thus probably not unusual.

SPERMATOGENESIS.

The somatic number of chromosomes in the male is also ten, and as in the female these seem to be alike in size and shape.

Such chromosome counts were generally made in cells of the developing nervous tissue where division phases are common (Figs. 3 and 4).

Spermatogonial divisions seem to be completed with comparative speed, for specimens which show them are not plentiful. Just as in the somatic cells the number here is undoubtedly ten (Fig. 5).

The stage following the spermatogonia seems to be much longer in duration. The cells increase perceptibly in size during this time. The earliest phase observable shows some flocculent masses of lightly staining chromatin irregularly distributed through the nucleus. At one point, always at the periphery of the nucleus, there is a more deeply staining mass. Nothing concerning the structure of this can be made out and its shape is variable (Fig. 8). With progressive development this deeply staining mass undergoes a few, very definite, changes. In successive steps it appears that a number of more or less irregular lumps is evolved. Still massed at first, these gradually become separated and then it is certain that they are five in number (Figs. 8 to 11). It is at this latter stage that a split is occasionally visible in some of them, but with increasing condensation this again becomes obliterated. Throughout this development these five bodies retain a definite tendency to remain in close proximity to each other, and this tendency is one that persists also through subsequent stages.

In the meanwhile the flocculent and more lightly staining chromatin has also undergone development. Before the denser mass has become evolved into five distinct bodies, this chromatin has been transformed into a fine network of threads. Apparently these are polarized toward the dense mass (Fig. 9). Like the leptotene threads of other forms, these threads shorten and thicken, a process accompanied by a progressive increase of their staining intensity. Polarization is finally lost, and already at this stage it becomes apparent that the number of shortened threads is less than ten (Fig. 10). As the threads continue their process of shortening, they are counted with greater ease, and in such a stage as shown in Fig. 11 it becomes certain that they are five in number. Like the denser bodies, these sometimes show a longitudinal split.

Both the denser bodies as well as the threads continue progressive condensation, and the former reach their final form some time ahead of the latter (Fig. 12). They are then somewhat oblong in shape, and take the hæmatoxylin stain with great intensity and there can be no doubt of their chromosomal nature. Somewhat later the erstwhile threads have also assumed this form, and there are then ten of these bodies or chromosomes, identical in size and shape. Those first evolved continue to betray a certain affinity for each other, and in the metaphase plate constitute a central group around which the other five chromosomes become ranged in no definite order (Figs. 13 and 14). Aside from this very characteristic grouping, the only difference between the two sets of chromosomes that is apparent consists in the rate at which they evolve or the stage which is the starting point of their development.

Throughout this development, there has been no trace of a tetrad formation. The general features of the case indicate that the split which was spoken of as occurring at one stage is nothing more than preparation for the equation division or else something of the nature of the "Querkerbe" observable in lower Crustacea.

Division now occurs in ordinary manner and ten chromosomes go to each pole (Figs. 15 to 17). The arrangement of chromosomes in the daughter cells is not absolutely certain, although fig. 16 indicates that there also the characteristic grouping is retained. Figures like these are too rare to admit of any definite conclusion however. At any rate, the time in which such an arrangement persists must be very short, for the chromosomes are generally found in a more or less irregular heap (Fig. 18).

The division just described is undoubtedly equational in character. Following it there seems to be no intervening further development in the chromosomes of the daughter cells. Instead, they begin to scatter in a longitudinal direction. This process is not entirely irregular however for it results in their separation into two groups of five each (Figs. 18 to 22). It is a remarkable feature that these two groups are each characterized by a distinct and different arrangement of their component chromosomes. The group going to one pole assumes the form of a V or a

triangle, while the sister group which goes to the opposite pole is circular or lumped in arrangement (Figs. 21 and 22). This grouping is so constant and has been observed in so many specimens, that no mistake seems possible, and the conclusion seems inescapable that it is of some significance. The telophase of this anomalous division still shows traces of the arrangement, but these are soon lost as the chromosomes of each daughter cell distribute themselves around the periphery of the nucleus. Their number here is undoubtedly five (Fig. 24). This initiates the formation of the spermatids in which the chromosomes gradually loose their staining reaction. No study of the subsequent stages was made except to determine that there is no sign of degenerating or abortive cells nor a size dimorphism in the spermatozoa.

Somatic Chromosomes.

Returning to the somatic tissues, it may be remarked here that although the number of chromosomes in each sex is the same, their arrangement differs in the two sexes. This is especially noticeable in the developing nerve tract, where in the male the cells in the resting stage show a relatively large nucleolus like structure (Fig. 2). This is not to be seen in the same tissue in the female where cells show only the flocculent chromatin peculiar to that phase (Fig. 1). That the nucleolus-like structure in the male nerve cells is nothing but the group of five chromosomes mentioned in the description of the spermatogenesis becomes almost certain in metaphase plates found in the same tissue. Figs. 3 and 4 show such grouping without a doubt.

Exactly the same feature is observable in spermatogonial plates, though the size of these renders them less favorable (Fig. 5). In contradistinction, oogonial plates have no such arrangement, and even in such a late stage before division as shown in Fig. 6 the chromosomes are arranged in no definite order.

Discussion.

An interpretation of these observations is perhaps not out of place. It is here given with the idea that it should not affect the observations however it may be received and is advanced in a speculative way.

As has already been stated, oögenesis very probably follows ordinary lines. The ten chromosomes constituting the diploid number are composed of five homologous pairs, and these synapse and form tetrads. Reduction is very probably normal, and results in a pronucleus with five chromosomes.

In the spermatogenesis, the spermatogonial divisions, like the somatic divisions, also occur in orthodox manner. This is apparently not true of the meiotic divisions however. In explanation of these, the best hypothesis is one which views the various developments in the light of sex chromosomal behavior and is as follows:

The central group of chromosomes which appears in the growth stages of the male as the more densely staining mass contains sex chromatin, equally distributed among the five chromosomes. The remaining chromosomes, which stain lightly at first, represent what may be regarded as purely autosomal chromatin. Granting this, and the assumption does not appear unjust in the light of what has been described, the seemingly peculiar development becomes a natural consequence. Just as in the spermatogenesis of the various Orthoptera and Hemiptera, the sex chromosomes always stain more or less intensely, and as far as observable do not go through the various stages of thread formation. That such formation may occur earlier, or in a restricted sense even while the dense mass is still irregular in outline, is not ruled out by any means. The autosomal chromatin on the other hand goes through all the usual steps, culminating in the formation of five chromosomes. The sex chromatin contained in the five grouped chromosomes will tend to explain their grouped arrangement, since again as in the Hemiptera, multiple X or X and Y chromosomes show a tendency to remain in close proximity during development.

If now the sex chromosomes in *Pseudococcus nipæ* are regarded homologous in every way to the autosomes, except that each carries a certain amount of sex chromatin, the subsequent behavior is just as would be expected. I may mention here that such sex chromosomes would imply a more intimate union of sex and autosomal chromatin than is illustrated by such a case as

Mermiria (McClung, '05) where the sex chromosome and the autosomes are distinct, but the former is attached to one of the latter. It is at present unnecessary to go into the relation of the two conditions, though very possibly they represent two distinct steps in the phylogeny of sex chromosomes.

Their subsequent behavior is more or less analogous to that of the X Y pair in other forms. This pair does not form a tetrad in the ordinary sense simply because its members are not homologous, or better perhaps, because neither has a true synaptic mate. When as in the homozygous state both members of a pair of sex chromosomes are homologous, synapsis and tetrad formation occur just as in the autosomes. This fact is plainly borne out in the oögenesis of many Hemiptera (Morrill, '10) as well as in the growth and maturation phenomena of the eggs of *Pseudococcus nipæ*. It is thus to be assumed that if in the present case of the spermatogenesis of *Pseudococcus nipæ* the sex chromatin were distributed equally over the ten autosomes, the pairs would be homologous and tetrads would be formed in the usual way.

The cytological evidence indicates nothing that should render an equation division exceptional in nature, and it does indeed occur in the usual manner. The second division witnesses reduction in that the autosomes carrying sex chromatin go to one pole while the purely autosomal chromosomes go to the opposite pole. Taking recourse to a parallel case once more, attention may be drawn to the two X chromosomes in *Syromastes* which always go the same pole in reduction (Wilson, '09). Similarly, the multiple X of the Reduviidæ always goes to one pole, although this is not an exactly parallel case since it is probably the product of fragmentation of a single X.

Thus to repeat what has already been intimated for the present case, the distribution of the chromosomes to their respective poles in the reduction division may be explained on the ground that we are concerned with five pairs of chromosomes. The members of each pair are homologous except for the fact that one of them in each instance carries a certain amount of sex chromatin. The presence of the latter does not influence the behavior of the chromosome pairs in reduction and the members of each pair go

to opposite poles. Its presence does however prevent haphazard distribution in that the five chromosomes carrying this sex chromation tend to remain clustered or grouped and therefore go to the same pole.

Although more or less contrary to the cytological evidence furnished by other groups of insects, it may not be amiss to suggest the possibility that in animals with haploid males each chromosome carries a certain amount of sex chromatin. It follows that the diploid female would then represent 2 X, whereas the haploid male would represent 1 X. In the haploid male the reduction division is not truly abortional as has been supposed, but is merely a division in which these sex chromatin carrying chromosomes go to one pole while the opposite pole receives no chromosomes simply because the mates to these chromosomes are absent. It is of interest to note that the straggling or lagging so often observed in the sex chromosomes of various insects is paralleled by the scattered and irregular distribution of the chromosomes on the spindle of this division in the Hymenoptera. And lastly, such irregular distribution is found also in the reduction division of *Pseudococcus nipæ*.

Pseudococcus nipæ thus would stand half way between forms with haploid males where every chromosome carries sex chromatin, and forms in which the sex chromatin is carried in very few chromosomes and there is little numerical variation in the chromosomes of the two sexes. In other words, half of the chromosomes in the males carry sex chromatin.

Although superficially an instance of Weismann's postulated ideal type of reduction in which the diploid number of chromosomes is halved without previous syndesis, the spermatogenesis of *Pseudococcus nipæ* nevertheless follows the commonly accepted lines of meiosis. The apparently exceptional behavior can be explained as due to an extreme mode of sex chromatin distribution and is not a unique example of the *Primærtypus* of reduction. It may be remembered that Goldschmidt ('05 and '08) gave this name to an instance of Weismann's simple type which he thought to have discovered in *Zoögonus mirus*. The Schreiners ('08) examining Goldschmidts slides believed to have

found a serious error in his counts of somatic chromosomes, which they believed in reality to be 24 and not 10 as he had reported. Furthermore, reduction occurred in the ordinary way, just as in *Tomopteris*. Gregoire ('09) in going over the same slides maintained that the Schreiners were correct in that the case was one of ordinary reduction, but that they in turn had made an error in the chromosome counts. The somatic number is about 12, and the reduced number 6. Lastly Wassermann ('11, '12, and '13) procured new material and concluded that Gregoire's counts had been correct. He did not agree with Gregoire as to the mode of synapsis however, and apparently was unable to reach a final conclusion in this regard himself. Although he thus does not believe that the question has received a definite settlement, the fact remains that Zoögonus does not represent the simple type of reduction that Weismann advanced in a hypothetical way.

If my hypothesis is correct, the male of *Pseudococcus nipæ* is heterozygous in that it has five sex-chromatin carrying chromosomes and five chromosomes purely autosomal in character. Crossing over would not occur in these chromosomes. It would occur however in the female, in which the ten chromosomes are composed of five homologous pairs. If the male represents 1 X, the female with ten sex-chromatin carrying chromosomes represents 2 X.

Summary.

1. The diploid number of chromosomes in *Pseudococcus nipæ* is ten in both sexes.

2. In the maturation of the egg, five tetrads are formed and reduction is probably normal.

3. In the spermatogenesis, five chromosomes are developed before the others, and these tend to remain grouped together.

4. No tetrads are formed, and in reduction five chromosomes go to one pole (supposedly those evolved first) and five to the other.

5. Explanation of this seemingly anomalous behavior is to be sought in the fact that five of the chromosomes carry sex chromatin.

6. The case is not so much to be regarded as an illustration of Weismann's ideal type of reduction, as an exceptional example of reduction due to unusual sex chromatin distribution.

BIBLIOGRAPHY.

Goldschmidt, Richard.

'05 Eireifung, Befruchtung, und Embryonalentwicklung des *Zoögonus mirus*. Zoöl. Jahrb., Bd. 21.

'08 Die Chromatinreifung der Geschlechtszellen des *Zoögonus mirus* und der Primärtypus der Reduktion. Arch. f. Zellf., Bd. 2.

Gregoire, Victor.

'09 Le réduction dans le *Zoögonus mirus* Lss. et le "Primärtypus." La Cellule, Tome 25.

McClung, C. E.

'05 The Chromosome Complex of Orthopteran Spermatocytes. BIOL. BULL., Vol. 9.

Morrill, Charles V.

'10 The Chromosomes in the Oögenesis, Fertilization, and Cleavage of Coreid Hemiptera. BIOL. BULL., 19.

Schreiner, A., und K. E.

'08 Neue Studien, V. Die Reifung der Geschlechtszellen von *Zoögonus mirus*. Vidensk. Selks. Schr. I. Math.-Naturv. Kl.

Wassermann, F.

'11 Ueber die Eireifung bei *Zoögonus mirus* Lss. Sitz.-Ber. d. Ges. f. Morph. und Phys., München.

'12 Zur Eireifung von *Zoögonus mirus*, ein Beitrag zur Synapsisfrage. Ver. d. Anat. Ges. Bd. 26.

'13 Die Oögenese des *Zoögonus mirus* Lss. Arch. mikr. Anat., Bd. 83, Abt. 2.

Wilson, E. B.

'09 Studies on Chromosomes. IV. Jour. Exp. Zoöl., 6.

All drawings made with a Spencer 15 eyepiece and Zeiss 1.5 objective with the exception of Figs. 1 and 2, where a 10 eyepiece and 2 mm. objective were used.

PLATE I.

1. Cells in nervous tissue of the female.
2. Cells in nervous tissue of the male.
3 and 4. Metaphase plates from nerve tissue of the male.
5. Spermatogonial plates.
6. Oögonial cell.
7. Tetrads prior to polar body formation in the egg.
8 to 12. Growth stages prior to first division.
13. Metaphase plate of first division.

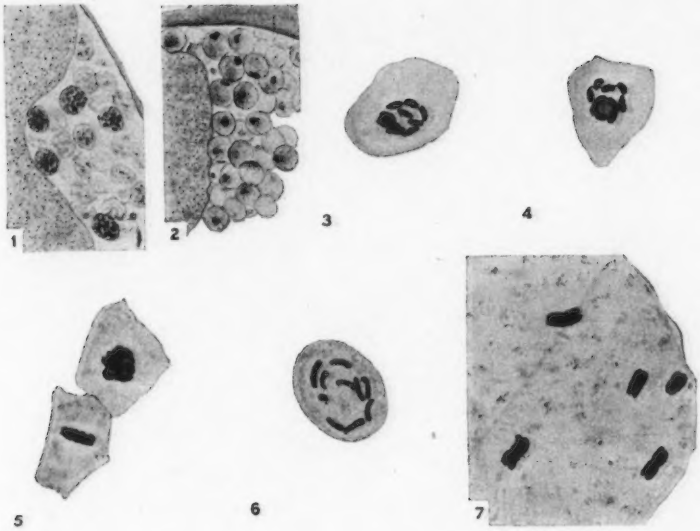

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PLATE II.

14. Metaphase plate of first division.
15. Side view of plate.
16 to 18. First division (equational).
19 to 23. Second or reduction disvision
24 and 25. Spermatids.

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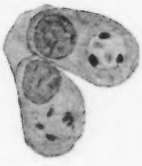

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FRANZ SCHRADER.

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OBSERVATIONS ON THE LARVÆ OF CORETHRA PUNCTIPENNIS SAY.

CHANCEY JUDAY.[1]

INTRODUCTION.

As part of a general problem relating to the biological productivity of lakes, a quantitative survey of the bottom fauna in the deeper portions of Lake Mendota at Madison, Wisconsin, was made between the early part of May, 1916, and the middle of August, 1918. This survey included only the macroscopic forms, such as the insect larvæ, the Oligochæta, and the Mollusca. The investigation showed that the full-grown larvæ of *Corethra punctipennis* Say constitute the principal element of the bottom population in the daytime during the greater part of the year. For at least three quarters of the year, in fact, they not only far outnumber all of the other forms combined, but they also exceed them in total weight. The great abundance of these larvæ thus makes them a very important factor in the biological complex of the lake.

Samples of the bottom were obtained by means of a modified form of the Ekman dredge; the opening of this instrument covered an area of 473 square centimeters. The mud obtained in each haul of the dredge was washed through a gauze net having meshes fine enough to retain all of the macroscopic forms. The material secured by the net was transferred to a jar and was then taken to the laboratory where the various organisms were sorted out and enumerated in the living state. The average live and dry weights of the various forms were also obtained, as well as the percentage of ash.

Observations were made at five regular stations located in water having a depth of 20.5 meters to 23.5 meters. These stations were widely separated in order to secure a fair average of the density of the bottom population in the deeper portions of the

[1] Notes from the Biological Laboratory of the Wisconsin Geological and Natural History Survey No. XXI.

lake. The results obtained at only one of these stations, designated as Station II., are considered here, however, because the other four were not visited regularly during the winter months. From April to June inclusive, the number of larvæ found at Station II. was from 10 per cent. to 20 per cent. larger than the general average of the five stations during these months, but in August the general average was larger than the numbers at Station II. In the six sets of averages obtained for the last three months of the year in 1916 and 1917, three of the averages for Station II. were larger than the corresponding averages of the five stations and three were smaller. Thus, the numbers obtained at Station II. were somewhat larger than the general average for the deeper part of the lake as a whole during the first half of the year, but they were somewhat smaller from July to September and substantially the same from October to December.

Numerical Results.

The average number of *Corethra* larvæ per square meter of bottom is shown for the different months of the year in Table I. Large numbers of these larvæ live over winter; in fact they are

Table I.

The Number of Corethra Larvæ per Square Meter Obtained from the Mud in the Daytime at Station II. during the Different Months of the Year.

In all months except January and February the numbers represent averages of two to nine samples.

Year.	January.	February.	March.	April.	May.	June.
1916.....					17,300	4,550
1917.....	25,340	23,740	30,380	23,230	17,900	16,000
1918.....		23,440	20,160	18,940	18,170	9,430
Year.	**July.**	**August.**	**September.**	**October.**	**November.**	**December.**
1916.....	3,380		7,400	17,600	26,900	26,900
1917.....	6,080	800	3,740	11,500	17,700	24,800
1918.....	2,820	960				

more numerous from November to April than at any other time of the year. During this interval the numbers range from approximately 18,000 to 30,000 individuals per square meter. At

this time of the year there is no loss from pupation and the losses from other causes are not great enough to reduce the number of these larvæ very materially, so that the number remains uniformly high during this period of time.

The ice usually disappears from the lake during the first week in April and soon after this event the larvæ begin to pupate. As the temperature of the water rises, the rate of pupation increases so that an appreciable decrease in the number of larvæ is noted for the month of May. With the further advance of the season, pupation becomes still more common and this results in a very marked decrease in the number of *Corethra* larvæ in late June as in 1916 and in 1918, or in early July as in 1917. This decline in numbers continues until the minimum of the year is reached in August, more especially during the first half of this month. A minimum of 295 larvæ per square meter was noted at Station II. on August 2, 1917, while the average in March of this year was a little more than one hundred times as large. (See Table I.)

Small swarms of adults appear in May and in early June, but the great flights are correlated in time with waves of very active pupation in late June, in July, and in early August. Thus, enormous swarms appear from time to time during the latter period.

During late August and especially in September there is a slackening in the process of pupation and correlated with this is an increase in the number of larvæ. The increase is most marked during the second half of September and in early October, but the numbers do not reach the maximum point until November or December. The largest number of larvæ obtained in any of the samples was 33,800 individuals per square meter on December 21, 1917.

Pupæ were not noted in the samples of mud until about the middle of June, or at the beginning of the more active period of pupation; thereafter they appeared regularly until late August. A maximum of 2,890 pupæ per square meter was found on June 28, 1917, while the second in rank was 1,370 individuals per square meter on July 9, 1917.

Deposition and Development of Eggs.

According to Muttkowski the adults emerge at night, "beginning early in the evening and continuing through the night. In the morning, if the lake is quiet, the females can be seen on the surface, ovipositing through the surface film." Eggs deposited by females kept in insect cages sink to the bottom of the aquarium and experimental evidence indicates that those deposited at the surface of the lake also sink to the bottom. Mud from Station II. where the water is 23.5 meters deep and also from Station I., located in water 18.5 meters deep, was washed through a sieve with meshes fine enough to remove all of the larvæ; this sifted mud was then placed in aquaria. At the end of five days a dozen small *Corethra* larvæ had appeared in the material from Station II., while five small larvæ were noted in the other bottom material at the end of a week, thus showing that the mud from both stations contained eggs.

Eggs that were deposited by females kept in captivity hatched within forty-eight hours when the temperature of the laboratory ranged from 21° to 24° C. The temperature of the lower water in the deeper portions of the lake is much lower than this, however, and the eggs which reach the bottom in these areas probably do not develop so rapidly. The bottom temperature at Station II. in summer, for example, ranges from slightly more than 9° in some years to about 14° in other years. On the other hand, eggs deposited in water not exceeding five meters in depth are subject to temperatures of 20° to 25° in July and August so that they probably hatch about as promptly as those kept under laboratory conditions.

Another factor that may retard development in the deeper water is the absence of free oxygen. Usually all of the dissolved oxygen below a depth of 18 meters is used up by the middle of July, after which no oxygen is available in this region until October. Thus, all of the *Corethra* eggs which reach the bottom in water that is 18 meters deep or more during this period must develop under anaërobic conditions if they develop at all. This anaërobic stage covers the greater part of the most active reproductive period of this insect and approximately 30 per cent. of

the area of the lake lies within the 18 meter contour. For two or three weeks in August, in fact, a little more than half of the lake bottom is subject to anaërobic conditions. No attempt was made to ascertain the effect of this lack of oxygen on the development of the *Corethra* eggs. Many cocoons of the Oligochæt *Limnodrilus* were noted in the bottom material during this period, however, and the eggs in them seemed to be developing normally in the absence of oxygen. This fact suggests that the eggs of *Corethra* may also develop normally under anaërobic conditions.

The young *Corethra* larvæ were not noted in the series of net catches until the last week in June, though the eggs of the first adults each year undoubtedly hatch at an earlier date than this. They were found regularly in the net catches from the latter part of June to the first week in October.

Behavior.

In 1917 and 1918 net hauls were made regularly at three of the stations before the mud catch was taken in order to see if any of the full-grown larvæ occupied the water in the daytime, but the results were entirely negative. Some of these hauls were made as early as 8:30 A.M. and others as late as 4:30 P.M., so that these observations covered the chief portion of the day. It was found also that the full-grown larvæ deserted the water on cloudy days as well as on clear days.

A series of observations made at Station II. during the afternoon and evening of July 16, 1917, showed that the full-grown *Corethra* larvæ had not emerged from the mud by 7:30 P.M., or just about sunset. At 8:00 P.M., or half an hour after sunset, 133 larvæ and 88 pupæ per square meter of lake surface were found in the water. By 8:30 P.M., or one hour after sunset, these numbers had increased to 3,945 larvæ and 442 pupæ. At the latter hour the full-grown larvæ had reached the surface of the lake, thus showing a vertical migration of 23.5 meters during an interval of about one hour.

A similar set of observations was made in 1920 beginning at 5:45 P.M. on June 10 and continuing until 5:30 A.M. on June 11. On the former date sunset came at 7:36 P.M., standard time, and sunrise on the following day at 4:18 A.M. No *Co-*

rethra larvæ were obtained from the water on June 10 until 7:15 P.M., at which time a catch yielded 22 individuals per square meter of lake surface. Fifteen minutes later, or just a few minutes before sunset, this number had risen to 176 larvæ per square meter, and by 7:50 P.M., or about a quarter of an hour after sunset, the number was 1,576. At 7:36 P.M. the larvæ had not invaded the upper 10 meters of water, but they had ascended to the 10–15 meter stratum. They did not appear at the surface until about an hour and a quarter after sunset, so that the rate of upward migration was somewhat slower than that noted in 1917. Pupæ reached the surface at 9:00 P.M., or approximately an hour and a half after sunset. The largest number of both larvæ and pupæ found in the water during this set of observations was noted in a catch taken at 10:00 P.M.; of the former there were 4,730 individuals per square meter of lake surface and of the latter 287. By 11:00 P.M. the numbers had declined to 2,100 and 110 respectively; the numbers were substantially the same as these at 2:00 A.M. on June 11.

Larvæ were still found in the upper meter of water at 3:30 A.M., but they had disappeared from the upper 10 meters by 3:47 A.M. and only one individual was obtained in a catch taken from the 0–15 meter stratum at 3:50 A.M. Practically, then, they deserted the upper 15 meters of water during a period of about 20 minutes. It should be noted, also, that this downward migration was not due to direct sunlight since it took place at least half an hour before sunrise. The larvæ were still occupying the 15–23 meter stratum in considerable numbers, since a catch at 3:55 A.M. yielded 1,658 individuals per square meter in that region; the same catch contained 88 pupæ per square meter also. The number of larvæ in the lower water then gradually diminished, the last disappearing between 4:45 and 5:00 A.M. According to these results, then, the full-grown *Corethra* larvæ enter the bottom mud by the end of the first half hour after sunrise and they remain there until about sunset.

Samples of mud taken at 6:00 and at 7:00 P.M. on June 10, 1920, yielded an average of 2,720 larvæ and 55 pupæ per square meter of bottom; as a result of the migration into the water these numbers had declined to 1,400 larvæ and 22 pupæ per square

meter at 8:00 P.M., while the samples obtained during the next three hours yielded from 1,600 to 2,100 larvæ. The latter number was also found at 3:00 A.M., but it rose to 2,665 at 4:00 A.M. and to slightly more than 3,000 per square meter at 5:00 A.M. Thus the mud contained from one half to two thirds as many larvæ at night as were found there in the daytime.

For a certain period after they hatch out, the behavior of the young larvæ is very different in the daytime from that of the full-grown individuals; that is, the former occupy the lower water during the daylight hours instead of the mud, being found in the lower part of the mesolimnion and in the hypolimnion. The young larvæ migrate into the upper water at night just as the full-grown ones do. It has not been definitely determined just how long this difference in behavior lasts; only rarely was an individual found in the mud which was estimated to be only one third as large as a full-grown larva and frequently individuals were obtained from the water which were recorded as half grown. Thus, it appears that the young larvæ inhabit the lower water in the daytime instead of the mud until they are approximately one third grown, or perhaps a little larger. Muttkowski states that the larval period lasts from six to seven weeks in the summer broods; on this basis it may be estimated that the difference in behavior between the young and full-grown larvæ continues for the first ten days or two weeks of the larval period.

A series of catches was made with a plankton trap on August 2, 1917, for the purpose of ascertaining the vertical distribution of the small larvæ. The results are shown in Table II. No larvæ were found in the upper 8 meters, but they appeared at 10 meters and at greater depths. The maximum number, 489 individuals per cubic meter of water, was obtained at a depth of 18 meters, which was about the middle of the hypolimnion. Somewhat more than 88 per cent. of the total number of individuals occupied the 15–20 meter stratum.

Some results obtained on Devils Lake, Wisconsin, show that the behavior of the full-grown larvæ of *Corethra plumicornis* Fabricius[1] differs in the daytime from that of *C. punctipennis* in

[1] Dr. J. R. Malloch kindly identified this larva.

Table II.

The Number of Young Corethra Larvæ per Cubic Meter of Water at Different Depths of Lake Mendota on August 2, 1917.

Those obtained at 10 meters and 12 meters were recorded as very small and for the other depths the individuals were estimated to be from a quarter to a third as large as full grown larvæ.

Depth in Meters.	Temperature, Degrees C.	Number of Larvæ per Cubic Meter.
8	19.8	0
10	17.4	44
12	16.0	67
15	14.5	200
18	13.6	489
20	13.5	311
23	13.3	22

Lake Mendota. In the former lake two net catches on May 25, 1917, which were made in the deepest water, namely, 14 meters, gave an average of 422 full-grown *C. plumicornis* larvæ per square meter of surface, while two hauls of mud at the same place yielded an average of 433 individuals per square meter. That is, these larvæ were substantially equally divided between the water and the mud at about 10:00 A.M. on a bright morning when the water was so transparent that a white disc 10 centimeters in diameter did not disappear from view until it reached a depth of 8.6 meters. In other words, the day distribution of the larvæ of *C. plumicornis* was practically the same in Devils Lake as the nocturnal distribution of the larvæ of *C. punctipennis* in Lake Mendota.

While the larvæ of *Corethra punctipennis* give a prompt negative reaction to light, yet it hardly seems probable that their extensive depth migration in Lake Mendota, even including a descent into the mud, is a simple light phenomenon. The transparency of the water is usually low in summer; a white disc 10 centimeters in diameter generally disappears from view at a depth of two meters to about four meters at this season of the year, which indicates that the light is cut off rather rapidly by the upper strata of water. On the morning of June 11, 1920, for example, the disc reading was 4.25 meters. A pyrlimnimeter has been used to determine the rate at which the sun's energy is cut off by the upper strata of the lake. The results obtained with this instru-

ment indicate that the intensity of the illumination at a depth of 23 meters on a clear day, between 11:00 A.M. and 1:00 P.M., is about equal to that produced by full moonlight at the surface of the lake. During the early forenoon and the late afternoon, as well as on cloudy days, the illumination is much smaller than this. For some time before sunset, the bottom stratum must be substantially in total darkness, yet the observations show that the emergence of the larvæ from the mud is very closely correlated in time with the setting of the sun.

Not only does the illumination in the bottom water become very small in the late afternoon, but there is a further protection from light afforded by the bottom ooze in which the larvæ remain concealed during the day. To what depth the larvæ penetrate the loose mud is not known, but in the laboratory they readily burrow down to a depth of a centimeter or more. The dim light which reaches the bottom in the deeper portions of the lake can penetrate the ooze only to a very slight extent at most, even during the brightest part of the day, and this raises the very interesting question as to what stimulus causes the larvæ and pupæ to emerge from the mud so promptly and regularly about the time of sunset. No definite data bearing on this point have yet been obtained.

These larvæ are eaten with avidity by many fishes and their habit of occupying the mud in the daytime may thus serve a very important purpose from the standpoint of protection from such enemies. A further protection is afforded by the disappearance of the dissolved oxygen in the hypolimnion. Usually by the first of August very little free oxygen remains in this stratum, which makes the lower water unfit for the permanent occupation of the larger forms which prey upon these larvæ. In spite of the lack of oxygen, however, Pearse and Achtenberg found that the yellow perch—*Perca flavescens* (Mitchill)—invades the lower water and feeds upon these larvæ. While these fish survive for a period of two hours in water that contains no dissolved oxygen, these authors state that it is doubtful whether a perch is able to feed for more than a few minutes at a time under such conditions. It seems probable, therefore, that the *Corethra* larvæ are not eaten as freely as they might be if anaërobic conditions did not

prevail in the lower strata of the deeper water. Also, the absence of dissolved oxygen in the hypolimnion serves as a protection to the young larvæ which occupy this region in the daytime for a certain period after they hatch out.

Number in Shallower Water.

The larvæ of *Corethra punctipennis* show a decided preference for the deepest portion of Lake Mendota. In the daytime, they are much more abundant in the mud where the water reaches a depth of 20 meters or more than they are in the shallower areas. It was found that the average number of larvæ within the area bounded by the 20 meter contour line was more than three times as large as the average for the region lying between the 8 meter and the 20 meter contours, while the number obtained in areas where the water did not exceed five meters in depth was practically negligible.

Some three hundred samples were taken in series which extended from the shallow water to the deep water; that is, from a depth of 8 meters or 10 meters down to a depth of 20 meters. The results of four sets of these observations are shown in Table III. It will be noted that there was a marked increase in the

Table III.

The Number of Corethra Larvæ per Square Meter of Bottom at Different Depths in Four Sets of Observations which were Made in 1917.

Date.	Depth in Meters.	Number.	Date.	Depth in Meters.	Number.
May 15.....	10.5	820	September 24..	10	110
	12.5	1,600		12	250
	15.5	4,640		15	5,500
	18	4,810		18	7,490
	20	7,800		20	13,380
June 22.....	10	100	October 24.....	12	85
	12	85		15	2,740
	15	1,080		18	11,650
	18.5	1,710		20	15,930
	20.5	3,010			

number of larvæ correlated with the increase in the depth of the water. On May 15, for example, the sample taken at 15 meters yielded about six times as many as the one at 10 meters, while

that at 20 meters gave nearly ten times as many as the latter. On September 24, the differences were fiftyfold and more than a hundredfold, respectively, and on October 24 the number was nearly two hundred times as large at 20 meters as at 12 meters.

Just how these larvæ are able to constantly maintain such a marked difference in numbers in favor of the deep water is a puzzling question. Their method of locomotion would not lead one to expect them to travel very far of their own accord should they reach the shallow areas, yet it seems probable that many of them are carried into the shallow water by the currents when they migrate into the upper strata at night. This would be true especially on windy nights. Table III. shows that a very small number of larvæ is found at 10 meters as compared with the deep water and 39 per cent. of the area of the lake lies outside the 10 meter contour line. The number is usually not much larger at 12 meters than at 10 meters and the former divides the area of the lake approximately into halves. The outer or shallower half of the lake, then, is very sparsely populated by these larvæ, but it is not clear just how the number is kept so small in comparison with the inner or deeper half of the lake.

In a large proportion of the former area the bottom does not consist of material in which the larvæ can readily conceal themselves in the daytime, being composed of sand, gravel, and rock, so that the tendency would be to avoid these areas. On the other hand, the larvæ are no more abundant in the shallow portions of protected bays where a muddy bottom suitable for concealment is found at a depth of only 5 meters or 6 meters. The difference can scarcely be attributed to a proportionally unequal distribution of eggs between the two regions because very large numbers of egg bearing females are found over the shallow water as well as along the shore; it seems probable, therefore, that enormous numbers of eggs are deposited in the shallow areas.

When the larvæ migrate into the upper strata of the lake at night, the direct currents tend to carry them into the shallow water, but the return currents, on the other hand, will aid more or less in bringing them back to the deep water. Apparently the chief factors governing the distribution of the *Corethra* larvæ

between the shallow half and the deep half of the lake are (1) an active migration, (2) the currents—direct currents on the windward side of the lake and return currents on the leeward side, (3) a relatively greater loss in the shallow water due to predatory enemies.

Number in Other Lakes.

For purposes of comparison similar quantitative studies of the bottom population were made regularly in Lake Monona and in Lake Waubesa during 1917. The former is only one kilometer from Lake Mendota and has nearly as great a maximum depth, namely, 22.5 meters. Lake Waubesa lies about seven kilometers southeast of Lake Mendota, but it is a much shallower body of water, having a maximum depth of only a little more than 11 meters. In Lake Monona only about one tenth as many *Corethra* larvæ were found as at corresponding depths and times in Lake Mendota; in some instances the difference was more than a hundredfold in favor of the latter lake. In the deepest part of Lake Waubesa the number varied from about the same as that at 11 meters in Lake Mendota to only a third or a quarter as many; but the deeper water of Lake Mendota yielded from forty to a hundred times as many larve as the deepest portion of Lake Waubesa. Bottom material has been obtained from about a dozen other Wisconsin lakes and in all of them the *Corethra* population has been relatively small, which seems to indicate that Lake Mendota offers a particularly favorable habitat for these larvæ.

Gravimetric Results.

Between June, 1916, and April, 1917, more than fourteen thousand larvæ of *Corethra punctipennis* were picked out of the material collected in Lake Mendota and they were dried for the purpose of making a chemical analysis of them. The average amount of dry matter per individual for this number was 0.251 milligram. The average weight was also determined for eleven other lots of larvæ containing from 100 to 300 individuals each. These averages ranged from a maximum of 0.311 milligram per larva, dry matter, in June to a minimum of 0.182 milligram in early September. The results of these weighings are shown in

Table IV. The higher average of dry matter in the June material may be due to a larger proportion of chitin in the larvæ just before they pupate. In August and early September the average size of the larvæ seems to be smaller than that of the winter brood and this is confirmed by the weights. At the height of the pupating season the summer larvæ pupate when they are distinctly smaller than the individuals which live over winter. The live weights of the smaller lots were also determined, as shown in Table IV., and they indicate that about 91 per cent. of the living animal consists of water.

The live weight of the June pupæ was only about 11 per cent. larger than that of the June larvæ, but the dry weight of the former was nearly twice as large as that of the latter. (See Table IV.) This marked difference in the dry weight was probably due to the presence of a larger amount of chitin in the pupa.

TABLE IV.

THE AVERAGE WEIGHT OF A SINGLE INDIVIDUAL OF CORETHRA PUNCTIPENNIS IN MILLIGRAMS, TOGETHER WITH THE PERCENTAGES OF WATER AND OF ASH.

Form.	Month.	Live Weight in Milligrams.	Dry Weight in Milligrams.	Per Cent. of Water.	Per Cent. of Ash.
Larva....	February...	3.06	0.250	91.72	7.06
	May.....	3.30	0.264	92.12	7.96
	June.....	3.15	0.311	89.13	7.33
	September..	2.57	0.182	92.93	9.53
	October....	2.83	0.264	90.66	8.62
	November..	3.20	0.285	91.03	8.10
Pupa.....	June.....	3.52	0.574	83.71	5.80
Adult.....	June.....	0.75	0.427	43.32	5.89

The adults yielded a much smaller live weight than either the larvæ or the pupæ because they possessed a much smaller proportion of water. Their dry weight was greater than that of the larvæ but smaller than that of the pupæ. The adults used for this weight were obtained from a large swarm on June 29, 1918, when pupation was very active, but there was no means of ascertaining their age; their weight probably decreases somewhat with age, and they live for a period of three to five days.

The ash of the larvæ varied from a minimum of about 7 per

cent. of the dry weight to a maximum of 9.5 per cent., the former being noted in February and the latter in September. The pupæ and adults yielded substantially the same percentages of ash, but these percentages were much smaller than in the larvæ.

There is more or less overlapping of the summer broods, which makes it difficult to estimate the number of larvæ produced during this season, but the winter crop of larvæ may be estimated with some degree of accuracy. In this investigation twenty-two samples of mud were obtained at the five regular stations in deep water during the month of November and they yielded an average of 17,350 *Corethra* larvæ per square meter of bottom. Five samples were secured in December also, and they gave an average of 21,900 individuals per square meter; but four of these samples were taken at Station II. which usually gave a larger yield than the other four stations. According to these figures, the early winter population of *Corethra* larvæ within the 20 meter contour may be conservatively estimated at 18,000 individuals per square meter. Between October and May the live weight averaged 3.1 milligrams per larva and the dry weight 0.266 milligram. Applying these weights to the above population gives a live weight of 55.8 grams per square meter, or 558 kilograms per hectare, which is equivalent to 497 pounds per acre, and a dry weight of 4.8 grams per square meter, or 48 kilograms per hectare, equivalent to 42.7 pounds per acre.

Muttkowski states that there may be two generations of summer larvæ in addition to the winter generation; but, since the former average somewhat smaller in size than the latter, the total weight of the summer broods is probably not greatly in excess of that of the winter brood. That is, a live weight of 1,200 kilograms per hectare (1,070 pounds per acre) would be a conservative estimate for the total annual production of *Corethra* larvæ in the deeper part of Lake Mendota; on this basis the dry weight would amount to somewhat more than 100 kilograms per hectare, or approximately 90 pounds per acre. These figures apply only to that portion of the lake which lies within the 20 meter contour line, since the larvæ are found in very much smaller numbers in the shallower water.

The 20 meter contour encloses an area of 664 hectares which would give an annual crop of larvæ amounting to substantially 797 metric tons, live weight, for this portion of the lake, or a dry weight of about 67 metric tons. The live weight of all other macroscopic inhabitants of this area was 92.3 metric tons and their dry weight was about 19 metric tons.

As previously indicated, the population of *Corethra* larvæ in the region between 8 meters and 20 meters averaged about one third as large per unit area as that in the deeper water. In order not to overestimate the annual production of the shallower water, the area lying between the shoreline and a depth of 10 meters may be omitted from the calculation since the number of larvæ found in this region is small; in addition, also, the average between the 10 meter and 20 meter contours, comprising an area of 1,738 hectares, may be reckoned as one quarter instead of one third as large as that of the deep water. On this basis the live weight becomes 300 kilograms per hectare and the dry weight 25 kilograms, thus making the annual crop of *Corethra* larvæ in this portion of the lake a little more than 521 metric tons, live weight, or about 43 metric tons of dry material. These results combined with those obtained for the deep water area give a total annual production of 1,318 metric tons of living larvæ which would yield 110 metric tons of dry material.

Chemical Results.

The results of the chemical analysis of the larvæ are shown in Table V. and they are stated in percentages of the dry weight.

Table V.

Results of the Chemical Analysis of the Larvæ of Corethra punctipennis Stated in Percentages of the Dry Weight.

Nitrogen.	Crude Protein (N×6.25.)	Ether Extract (Fat).	Crude Fiber (Chitin)	Per Cent. Ash.
10.74	67.12	9.45	6.15	7.96

The percentage of nitrogen is notably high, which means a correspondingly large proportion of crude protein. The percentage

given in the table does not include the nitrogen in the crude fiber (chitin) which amounted to 0.46 per cent. In comparison with this the larvæ of *Chironomus tentans* yielded a much smaller percentage of nitrogen, namely, 7.36 per cent.

The larvæ yielded a fairly large amount of fat (ether extract), namely 9.45 per cent. of the dry sample. Together the crude protein and the fat constituted more than 76 per cent. of the dry material. From the standpoint of quality, this large proportion of these two excellent food materials gives the larva of *Corethra punctipennis* a very high rank as a source of food for other organisms.

LITERATURE.

Birge, E. A., and Juday, C.

'11 The Inland Lakes of Wisconsin. The dissolved gases of the water and their biological significance. Wisconsin Geological and Natural History Survey, Bulletin No. XXII, pp. xx + 259. Madison.

Juday, C.

'04 The Diurnal Movement of Plankton Crustacea. Trans. Wis. Acad. Science, Arts and Let., Vol. XIV., Part 2, pp. 534–568. Madison.

'08 Some Aquatic Invertebrates that Live under Anaërobic Conditions. Trans. Wis. Acad. Science, Arts and Let., Vol. XVI., Part 1, pp. 10–16. Madison.

Muttkowski, R. A.

'18 The Fauna of Lake Mendota. Trans. Wis. Acad. Science, Arts and Let., Vol. XIX., Part 1, pp. 374–482. Madison.

Pearse, A. S., and Achtenberg, Henrietta.

'20 Habits of Yellow Perch in Wisconsin Lakes. Bulletin of the Bureau of Fisheries, Vol. XXVI., pp. 295–366. Washington.